Interspecific Mating in Blattaria[1]

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ABSTRACT

No matings occurred in the laboratory between species of 4 genera *(Blaberus, Byrsotria, Eublaberus,* and *Archimandrita)* of Blaberinae. Although several matings took place among 4 species of *Blaberus,* and among 5 species of *Blattella,* mechanisms responsible for reproductive isolation were quite effective among the above genera of Blaberinae, 4 species of *Blaberus,* and 7 species of *Blattella.* Almost invariably, eggs deposited by interspecifically mated females did not develop.

When he used female sex pheromones of several genera and species of cockroaches, Barth (1961[2]) found that the female attractant of *Periplaneta americana* (L.) would stimulate males of *P. brunnea* Burmeister, *P. fuliginosa* (Serville), and *Blatta orientalis* L., but not *Eurycotis floridana* (Walker), *Byrsotria fumigata,*[3] *Leucophaea maderae* (F.), and *Nauphoeta cinerea* (Olivier). The female pheromone of *B. fumigata* evoked a positive response from *Blaberus craniifer* males, a weak response from *B. giganteus,* but none from *P. americana.* The pheromone from *B. craniifer* stimulated males of *Byrsotria fumigata.* Barth (1961[2]) concluded that "Within the Blaberinae, the female sex pheromones of *Byrsotria, Blaberus craniifer,* and *B. giganteus* are interspecifically effective in releasing male courting behavior in all combinations tested." Substances have been extracted (Roth and Dateo 1966) from bodies of 9 species of cockroaches (adult males, females, or nymphs) representing 9 different genera, which induced overt sexual behavior in females of *N. cinerea.* Hartman and Roth (unpublished observation) observed a female of *L. maderae* palpate the tergites of a courting male *N. cinerea,* a typical sex response of female cockroaches prior to mating.

Copulation in cockroaches is preceded by a series of maneuvers by both sexes which are released by chemical and/or tactile stimuli (Roth and Barth 1967). With few exceptions, the female of most species must palpate the male's exposed abdomen and assume a position above him before successful mating will occur. In these species, mating will not occur unless the female responds to the male's pheromone and actively accepts him.

The fact that a male cockroach responds to the pheromone of the female of another species, and vice versa, is no assurance that interspecific mating will occur, because copulation is dependent on the positive responses of both sexes. However, there are at least 2 instances in which crossing has occurred between different species of Blattaria. One case of mating between a female *Epilampra abdominigrum* (De Geer) and male *E. maya* Rehn has been recorded (Roth and Gurney 1969). Females of *Pycnoscelus surinamensis* (L.) will mate when confined with males of *P. indicus* (F.); these are sibling species, *surinamensis* being obligatorily parthenogenetic and apparently evolved from the bisexual *indicus* (Roth 1967b). In this paper I shall report the results of attempts to cross several species of Blaberinae and several species of *Blattella* (Blattellidae).

MATERIALS AND METHODS

In the tests with the Blaberinae, all of which are large, 1–5 ♂ of a species were kept with females of various other species (in mixed groups) from the time the females emerged until they mated, oviposited, or died. Some males were with females for several months; all females were kept with males longer than their normal precopulation period. Females were examined daily for the presence of spermatophores. With *Blattella,* individual females were kept in small beakers with 2 ♂ of a species until they mated, oviposited, died, or passed their normal precopulatory period. All males of species of *Blattella* have uricose glands and during copulation cover the spermatophore in the vestibulum of the female with a large plug of uric acid which is readily seen with

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[2] R. H. Barth, Jr. 1961. Comparative and experimental studies on mating behavior in cockroaches. Ph.D. thesis, Harvard University, Cambridge, Mass. 274 p.
[3] Authors for specific names that are not given in the text are indicated in the tables.

Table 1.—Interspecific matings in Blaberinae.[a]

Males	Females: *Blaberus* *craniifer* Burmeister	*Blaberus* *giganteus* (L.)	*Blaberus* *atropos* (Stoll)	*Blaberus* *discoidalis* Serville	*Byrsotria fumigata* (Guérin)	*Eublaberus posticus* (Erichson)	*Archimandrita tessellata* Rehn
craniifer	●●●●●		○	○○○○○○○○○	○○○○○	○○○○○	○
giganteus	●○○○	●●	○	●●○○○○○○○	○○○○○	○○○○○	○
atropos	○○○○○			○○○○○	○○	○○○○○	○
discoidalis	●●○○○	○○	●●○	●●●●●	○○○○○	○○○○○	○
parabolicus	●○○○○	○		●●●●●	○○○○	○○○○○	○
fumigata	○○○○○			○○○○○	●●●●	○○○○○	○○
posticus	○○○○			○○○○○	○○○	●●●●●	○
distanti	○○			○○○○○	○○	○○○○○	○
tessellata	○○○○			○○○○○	○○○	○○○○○	●●●●

[a] Each circle represents a single female. Solid circles = females mated. Open circles = females did not mate. No females of *B. parabolicus* Walker or *E. distanti* were available.

the naked eye (Roth and Dateo 1964, 1965; Roth 1967a). Mating in *Blattella* was determined by the presence of white uric acid on the genital segments of the female, male, or in the beaker.

RESULTS AND DISCUSSION

Table 1 summarizes the results with the Blaberinae. The only interspecific matings occurred between species of *Blaberus*. *B. giganteus* mated with *B. craniifer* and *B. discoidalis*. *B. discoidalis* mated with *craniifer* and *B. atropos*, and *B. parabolicus* mated with *craniifer* and *discoidalis*; it is noteworthy that *parabolicus* mated with all 5 ♀ of *discoidalis*. There were no intergeneric matings, even between *B. craniifer* and *Byrsotria fumigata* although, according to Barth (1961[2]) the female pheromones of these 2 species are intergenerically stimulating to males.

No prolonged periods of observation were made on the behavior of the males toward the females of the various species. However, in the course of examining females for spermatophores, a male of *B. parabolicus* was seen to court *B. giganteus*, a male of *Eublaberus distanti* (Kirby) attempted to mate with *B. craniifer*, and also courted *E. posticus* (pumped his wings, butted the female, and exposed his tergites to the indifferent female). No matings occurred between any of these combinations.

With 1 exception, none of the females which mated with males of a different species produced young, although some of them oviposited.[4] Several of these females were dissected long after a normal gestation period, and spermathecae were examined for sperm. The results were:

1. *B. craniifer* (♀) × *B. giganteus* (♂). Dissected 164 days after it mated, this female still retained the spermatophore which normally is ejected a few days after copulation. No sperm were in the spermathecae, and the female never oviposited; ovarian oöcytes were degenerating.

2. *B. discoidalis* (♀) × *B. giganteus* (♂). Female oviposited. No sperm in spermathecae.

3. *B. craniifer* (♀) × *B. discoidalis* (♂). One ♀ formed and aborted 2 oöthecae. Sperm were present. The 2nd ♀ carried its oötheca ca. 3½ months; the eggs were dead, but motile sperm were present in the spermathecae.

4. *B. atropos* (♀) × *B. discoidalis* (♂). One ♀ died ca. 3 months after ovipositing. The uterus contained an oötheca with 17 eggs, of which only 2 had developed. When freed from the oötheca, 1 of the developed eggs survived as a nymph (♀). This female nymph had 2n = 40 chromosomes (the metaphase chromosomes of 5 cells were counted). The 2n chromosome number of *atropos* (♀) = 74, and *discoidalis* (♂) = 37. If the aforementioned nymph actually resulted from this mating one might expect its chromosome number to be 56. Facultative parthenogenesis occurs in several species of cockroaches (Roth and Willis 1956). Although it is probable that the nymph resulted from an unfertilized egg, it had 3 more chromosomes than the haploid number (37) expected in *atropos*. A 2nd *atropos* female was dissected 3 months after it mated. Motile sperm were present but the oöcytes never developed.

5. *B. craniifer* (♀) × *B. parabolicus* (♂). The female was dissected ca. 4 months after it oviposited. The oötheca was small and abnormal, and no sperm were in the spermathecae.

6. *B. discoidalis* (♀) × *B. parabolicus* (♂). Of 4 ♀ dissected, only 1 had sperm. Two ♀ never oviposited and 2 had small oöthecae in their uteri.

Only a few interspecific matings occurred between species of *Blattella* (Table 2). *B. germanica* males mated with *bisignata* and sp. D. *B. lituricollis* mated with sp. C. Males of sp. D. mated with *bisignata, germanica,* and sp. C. A species E male mated with *lituricollis*. No offspring were produced by any of the females which mated to males of species other than their own.

Different species which do not mate in nature, though they may meet, may mate when confined together (Mayr 1942). There are several sexual

[4] The Blaberidae includes all ovoviviparous cockroaches. When these species oviposit, the eggs are extruded 2 by 2 and surrounded by a proteinaceous covering. The completed oötheca is then retracted into a uterus or brood sac where the eggs develop (Roth 1967c).

Table 2.—Interspecific crosses in *Blattella* spp.[a]

Males	Females: *bisignata* (Brunner)	*germanica* (L.)	*lituricollis* (Walker)	*sauteri* (Karny)	sp. *C*[b]	sp. *D*[c]	sp. *E*[d]
bisignata	●●●●●●○○○	○○○○○	○○○○○○○	○○○○○	○○○○	○○○○	○
germanica	●○○	●●●●●	○○	○○○○○	○○○○	●○○○○	○
lituricollis	○○○○○	○○○○○	●●●●●●●●●●○	○○○○○	●●○○○○	○○○○○○	○○○
sauteri	○○○○	○○○○	○○○	●●●●●	○○○○○○	○○○○○	○○
sp. *C*[b]	○○	○○○	○○	○○○	●●●●○	○○	○○○
sp. *D*[c]	●○○○○	●○○○○	○○○○	○○○○○	●○○○	●●●●●	○○
sp. *E*[d]	○	○○	●○○	○○○	○○○○	○○○	●●●○○

[a] Each circle represents a single female. Solid circles = females mated. Open circles = females did not mate.
[b] An apparently new species, from Salika Falls, Thailand.
[c] A species near *humbertiana* (Saussure), from India.
[d] A species from Uganda, Africa.

isolation mechanisms, and differences in behavior or sexual-releasing stimuli are important factors. Differences in size between the sexes of *Blaberus* might be an isolating mechanism to prevent crossing. But *giganteus* and *parabolicus* males are much larger than *discoidalis* females with which they mated; conversely *discoidalis* males are much smaller than *craniifer* and *atropos* females, and a few matings did occur between these species. It is unfortunate that larger numbers of some of the species of *Blaberus* were not available, but it is apparent that both sexes of several of the species respond to one another's pheromones, and in particular *parabolicus* males and *discoidalis* females; these species are capable of mating but are interspecifically infertile. The 5 species of *Blaberus* (Table 1) represent 2 of the 3 species Groups of this genus. *B. craniifer* and *giganteus* belong to the *Giganteus* Group, and *atropos, discoidalis,* and *parabolicus* are members of the *Atropos* Group (Roth 1969). Interspecies Group matings can occur in *Blaberus.*

With the exception of *B. parabolicus* males and *B. discoidalis* females, interspecific matings were relatively rare under the confined conditions of these experiments, and it seems evident that reproductive isolation mechanisms operating among several genera of Blaberinae and several species of *Blaberus* and *Blattella* are quite effective.

Although many factors may stand in the way of successful interspecific mating, once this mating occurs differences in chromosome numbers could be an important factor preventing egg development. Of the 5 species of *Blaberus,* 3 (*craniifer, giganteus,* and *atropos*) have 2n ♀ = 74 chromosomes, *discoidalis* has 38, and *parabolicus* has 40 (Cohen and Roth 1970). With the exception of 1 mating between *craniifer* and *giganteus,* all the interspecific matings of *Blaberus* involved species with different chromosome numbers. The 2n ♀ chromosome number of the *Blattella* spp. are: *bisignata* 24, *germanica* 24, *sauteri* 24, *lituricollis* 26, sp. *C.* 28, sp. *D* 30, and sp. *E.* 50 (Cohen and Roth 1970). Only 1 mating occurred between species having the same chromosome numbers (*bisignata* × *germanica*).

One observation regarding oviposition may be noted. Virgin females of the various species of *Blattella* frequently oviposit abnormally. Some do not oviposit at all or occasionally produce eggs which are extruded without an oöthecal covering. In *Blattella,* the oötheca is rotated 90° after it is formed, and the eggs are normally carried with their micropylar ends facing laterally. Rarely, in *B. germanica,* is the oötheca carried with the keel dorsad, or its rotation is incomplete (Roth 1967c). In the present studies I noted that an unusually high percentage of oöthecae of virgin *B. sauteri* were not rotated at all, and a few were incompletely rotated; of 22 oöthecae (from 17 virgin ♀), 12 (54%) were not rotated normally. I examined females from a culture of *sauteri* (where mating presumably occurred) and found 28 carrying rotated oöthecae and only 1 ♀ with a partially rotated oötheca. It would appear that mating (i.e., sperm in the spermatheca) probably plays some role in effecting normal rotation of the oötheca in this species. Stay and Gelperin (1966) showed that in the ovoviviparous *Pycnoscelus indicus* female, normal oviposition (i.e., retraction of the oötheca into the uterus) depends on the presence of sperm in the spermatheca.

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REFERENCES CITED

Cohen, S., and L. M. Roth. 1970. Chromosome numbers of the *Blattaria.* Ann. Entomol. Soc. Amer. 63:
Mayr, E. 1942. Systematics and the Origin of Species. Columbia Univ. Press, New York. 334 p.

Roth, L. M. 1967a. Uricose glands in the accessory sex gland complex of Blattaria. Ann. Entomol. Soc. Amer. 60: 1203–11.

1967b. Sexual isolation in parthenogenetic *Pycnoscelus surinamensis* and application of the name *Pycnoscelus indicus* to its bisexual relative (Dictyoptera: Blattaria: Blaberidae: Pycnoscelinae). Ibid. 60: 774–9.

1967c. The evolutionary significance of rotation of the oötheca in the Blattaria. Psyche 74: 85–103.

1969. The male genitalia of Blattaria. 1. *Blaberus* spp. (Blaberidae: Blaberinae). Ibid. 76: 217–50.

Roth, L. M., and R. H. Barth, Jr. 1967. The sense organs employed by cockroaches in mating behavior. Behaviour 28: 58–94.

Roth, L. M., and G. P. Dateo. 1964. Uric acid in the reproductive system of males of the cockroach *Blattella germanica*. Science 146: 782–4.

1965. Uric acid storage and excretion by accessory sex glands of male cockroaches. J. Insect Physiol. 11: 1023–9.

1966. A sex pheromone produced by males of the cockroach *Nauphoeta cinerea*. Ibid. 12: 255–65.

Roth, L. M., and A. B. Gurney. 1969. Neotropical cockroaches of the *Epilampra abdomennigrum* complex; a clarification of their systematics (Dictyoptera, Blattaria). Ann. Entomol. Soc. Amer. 62: 617–27.

Roth, L. M., and E. R. Willis. 1956. Parthenogenesis in cockroaches. Ibid. 49: 195–204.

Stay, B., and A. Gelperin. 1966. Physiological basis of oviposition behaviour in the false ovoviviparous cockroach *Pycnoscelus surinamensis* (L). J. Insect Physiol. 12: 1217–26.

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